DEFENSIVE ECOLOGY OF THE CRUCIFERAE[1]

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ABSTRACT

The glucosinolates (mustard oil glucosides), present in all crucifer species examined, seem to provide a major line of chemical defense against bacteria, fungi, insects, and mammals. Circumstantial evidence suggests that other classes of secondary compounds, each restricted to one or a few genera, represent a second line of chemical defense.

Survival of wild crucifers depends partly on escape from adapted enemies in time and space. Discovery of crucifers by several enemy species is aided by behavioral responses to glucosinolates or their breakdown products. Allylglucosinolate (sinigrin) in the leaves of *Thlaspi arvense* releases allylthiocyanate instead of the more typical allylisothiocyanate, which is used as a host-finding attractant by several insect species. This change in secondary chemistry may reduce the rate of discovery of *Thlaspi* plants by crucifer-adapted enemies.

The defensive ecology of crucifers seems to typify that of herbaceous plants generally: chemical resistance, in the form of small amounts of toxic compounds, combined with low apparency to enemies which are adapted to the chemical defenses. The importance of the Cruciferae and other families of herbaceous plants as sources of food-plants for man may result in large part from their relatively low concentrations of toxins. The mature foliage of trees, shrubs, and grasses, by contrast, remains poor food for man, just as for other plant enemies.

An important component of the defensive ecology of crucifers and other unapparent plants seems to be chemical diversity in space and time. Closer simulation of this diversity in fields of agricultural crops may reduce the need for synthetic pesticides.

The family Cruciferae comprises approximately 400 genera and 3,000 species, the vast majority of which are herbaceous (Vaughan et al., 1976). The greatest number of species are found in temperate regions of the northern hemisphere, especially in those with a Mediterranean type of climate. The Irano-Turanian region alone contains about 150 genera and 900 species and may well have been the evolutionary cradle of the family, at least in the Old World (Hedge, 1976). The family has colonized a great variety of habitats, including arctic and alpine regions and some of the most climatically inhospitable deserts, though it is poorly represented in the tropics (Hedge, 1976).
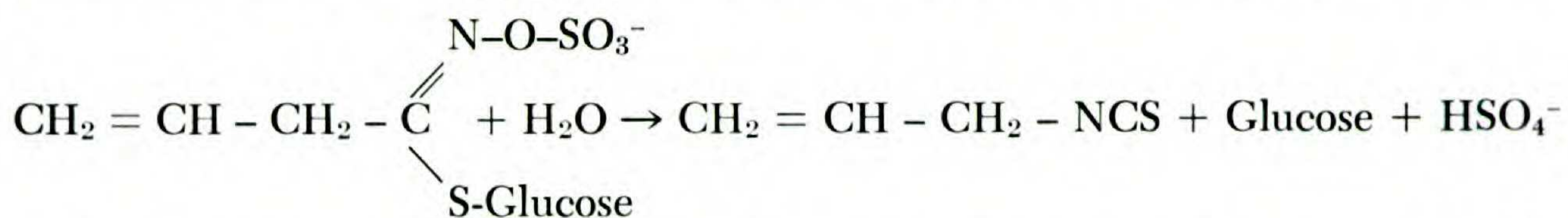
The family is the source of several economically important species and varieties, especially the cole crops of the genus *Brassica*. Economic incentives have stimulated extensive research on interactions between crucifers and their associated insects and pathogens. Understanding of the chemical aspects of these interactions has been helped greatly by unusually thorough knowledge of the family's chemistry (see Kjaer, 1976).

PRIMARY CHEMICAL DEFENSE

The first characteristic line of chemical defense in crucifers is evidently provided by the glucosinolates (mustard oil glucosides, thioglucosides). The occurrence of these compounds, more than 70 of which are known, is restricted almost entirely to the related families Capparaceae, Cruciferae, and Resedaceae. Approximately 300 crucifer species have been examined so far and all contain glucosinolates (Kjaer, 1960, 1976; Ettlinger & Kjaer, 1968). These compounds are hydrolyzed typically to yield volatile isothiocyanates (mustard oils) when plant tissues are damaged; allylglucosinolate (sinigrin), for example, is a major component of plants of the genus *Brassica* and breaks down to allylisothiocyanate:

$$CH_2 = CH - CH_2 - C \overset{\displaystyle N-O-SO_3^-}{\underset{\displaystyle S\text{-Glucose}}{\big\langle}} + H_2O \rightarrow CH_2 = CH - CH_2 - NCS + Glucose + HSO_4^-$$

Allylisothiocyanate, released from allylglucosinolate, is largely responsible for the odor of cooked cabbage (MacLeod, 1976). Hydrolysis of glucosinolates is catalyzed by a group of enzymes (myrosinases) which are stored separately within the plant tissues but which come into contact with their substrates when the plant tissues are bruised or otherwise damaged (Kjaer, 1976; Björkman, 1976). Storage of isothiocyanates in the form of glucosinolates may represent an adaptation to avoid autotoxicity; isothiocyanates are strongly phytotoxic (Hooker et al., 1945; Bell & Muller, 1973).

Glucosinolates or their breakdown products are known to be powerful antibiotics (Virtanen, 1958, 1965) and to inhibit the growth of fungi (Walker et al., 1937) and insects (Brown, 1951; Lichtenstein et al., 1964). The concentration of allylglucosinolate in the foliage of *Brassica nigra* plants in Tompkins County, New York, was found to be about 0.4% of fresh weight, depending somewhat on habitat and leaf age (P. Feeny and L. Contardo, in preparation); at this concentration the compound proved to be toxic to larvae of the black swallowtail butterfly, *Papilio polyxenes*, which naturally feed on umbellifers but occur in the same habitats as many crucifer species in the northeastern United States (Erickson & Feeny, 1974; P. Blau, P. Feeny and L. Contardo, in preparation). Glucosinolates or their hydrolysis products, when ingested in large quantities, are also toxic to mammals; the effect seems to result, at least in part, from the effectiveness of allylisothiocyanate as a tissue irritant (Kingsbury, 1964).

Glucosinolates in crucifers may play a role as allelopathic agents, inhibiting the germination and growth of competing plants. Patches within the annual grasslands of southern California are dominated by *B. nigra*, introduced from Europe. Bell & Muller (1973) showed convincingly that the persistence of these patches from year to year can be attributed to inhibition of the germination and growth of other plants by compounds leached from *B. nigra*. They found that allylisothiocyanate is a potent inhibitor of germination by seeds of several grasses but ruled it out as the allelopathic agent because of its rapid loss of activity in the soil. The unknown toxic compounds are water soluble and are leached from dead *B. nigra* tissues of the previous season's growth by the first fall rains, which

also serve as the stimulus for germination by the seeds of most species (Bell & Muller, 1973). I am not convinced that the authors have completely ruled out the possibility that the allelopathic agent is allylglucosinolate, stored in dead stems during the summer drought period and capable of releasing allylisothiocyanate over a period of time after being leached into the soil.

The available evidence thus suggests that the biological activity of the glucosinolates is broad and supports the contention that predation, disease, and perhaps competition are selective pressures which have contributed to the evolution and diversification of these compounds in the Cruciferae (see also Feeny, 1976).

THE CRUCIFER FAUNA

In spite of their content of glucosinolates, crucifers are attacked by an extensive array of insect species, several of which have become major pests of cultivated cruciferous crops. Many of the insect species which attack crucifers are "specialists" which rarely or never attack plants of other families; examples include larvae of the familiar cabbage butterfly, *Pieris rapae*, the cabbage aphid, *Brevicoryne brassicae*, and the cabbage flea beetles *Phyllotreta cruciferae* and *P. striolata* (Root, 1973). Generalist insects which include crucifers among their normal range of host-plants include the cabbage looper, *Trichoplusia ni*, and the green peach aphid, *Myzus persicae*. Crucifers are subject also to attack by an extensive array of fungi and bacteria (Westcott, 1971) and are probably eaten in significant quantities by wild mammals. In view of the deleterious effects of glucosinolates on organisms which do not normally attack crucifers we must presume that the various species making up the typical fauna of natural crucifers are somehow adapted to detoxify glucosinolates or otherwise avoid their harmful effects. The actual mechanisms of detoxification by adapted enemies are not yet known. Larval growth of the cabbage butterfly, *P. rapae*, on a wide range of crucifer species and cultivated varieties was compared recently by Slansky & Feeny (1977). Growth showed no obvious relationship to the varied pattern of glucosinolates present in the test plants but was closely related to the availability of nitrogen in the plant food. Individual glucosinolates vary in their toxicity to nonadapted insects (e.g. Brown, 1951); in crucifer-adapted insects, however, the extent to which tolerance of one glucosinolate confers tolerance of others needs to be examined in more detail.

When concentrations of allylglucosinolate in the leaves of collard plants, *Brassica oleracea*, were artificially increased by culturing to 20 times the typical level, growth of *P. rapae* larvae remained unaffected (P. Blau, P. Feeny and L. Contardo, in preparation). This result suggests that glucosinolates represent "qualitative" or "evolutionary" barriers to nonadapted insects: once overcome by adaptation they have little or no toxic effect in spite of wide variation in concentration (Feeny, 1975, 1976). This is consistent with the finding by van Emden (1972) that relative growth rate of the cabbage aphid, *B. brassicae*, was correlated positively with the "total allylisothiocyanate" content of crucifer test-plants. Glucosinolates stimulate feeding by this crucifer-restricted aphid but they are evidently not toxic to it, at least at concentrations normally encountered in the plants. Dosage-related toxicity of glucosinolates may have greater ecologi-

cal effects on crucifer-adapted bacteria and fungi than it seems to have on insects which specialize on these plants.

The effects of glucosinolates on generalist insects seem to be intermediate between their effects on crucifer-specialists and those on insects which do not naturally attack crucifers. The southern armyworm, *Spodoptera eridania*, and peach aphid, *M. persicae*, naturally attack crucifers as well as plants of many other families. They must therefore be able to tolerate at least low levels of glucosinolates. However, larvae of *S. eridania* have less tolerance for leaves artificially boosted with allylglucosinolate than have larvae of *P. rapae* (P. Blau, P. Feeny and L. Contardo, in preparation) and the relative growth rate of *M. persicae* is correlated negatively with the "total allylisothiocyanate" content of crucifer leaves (van Emden, 1972).

Escape from Adapted Enemies in Space and Time

Such is the ability of adapted enemies to damage and destroy crucifer plants, once they have been discovered, that the survival of crucifers in nature must surely be attributable in large measure to their ephemeral life histories which provide a constantly changing pattern of geographical and phenological distribution. The habitats most favored by crucifers seem to be those in which periods favorable for growth are severely limited by climatic variables such as rainfall (e.g. chaparral, grassland, desert) and temperature (arctic and alpine habitats). Typical crucifers must therefore be capable of rapid growth to maturity and seed-set, and it is perhaps not surprising that so many species have evidently been preadapted to exploit disturbed areas associated with human activities. Short growth season, shifting pattern of geographic distribution, and association with harsh and somewhat unpredictable climatic conditions are all characteristics which are likely to favor escape by plants from their adapted enemies (Janzen, 1970; Rhoades & Cates, 1976; Feeny, 1976).

The importance of escape from adapted insect enemies to the ecology of herbaceous plants was well illustrated by the history of introduced Klamath weed, *Hypericum perforatum*, in California (Huffaker & Kennett, 1959). In 1951 this plant infested more than 2 million acres of range land, covering up to 80% of the ground area in some places. Introduction from Europe of the *Hypericum*-adapted leaf beetles, *Chrysolina quadrigemina* and *C. hyperici*, reduced the plant to less than 1% of its former abundance by 1959. Both plant and beetles continued to persist at low densities, the plant surviving best in shadier habitats where the beetles are less effective (Huffaker & Kennett, 1959). "It would seem that the new low density of *Hypericum perforatum* is maintained at a level at which interplant distance restricts epidemic development of the beetle by limiting its opportunity to discover the isolated specific food plants" (Harper, 1969). While no such dramatic examples are available, it seems, for cruciferous plants, escape from discovery by adapted enemies is likely to be an important component of their defensive ecology also.

Pimentel (1961) and Root (1973) have shown that populations of crucifer-adapted specialists such as *B. brassicae* and *P. cruciferae* reach higher densities on collard plants grown in monoculture patches than on plants grown among di-

verse meadow vegetation. Root (1973) attributed these findings to "resource concentration": herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands. An individual collard plant is more "apparent" (i.e., susceptible to discovery) when growing next to other collard plants than when growing among plants of other families (Feeny, 1976). Comparable experiments by Smith (1976) showed that populations of *B. brassicae* and other crucifer-feeding species reached higher levels on Brussels sprout plants grown on weed-free soil than on plants grown among weeds. Trapping experiments showed that weed-free plants were more attractive to colonizing aphids, probably because a background of bare soil presents greater visual contrast than does a background of weeds (Smith, 1976). Diversity of surrounding vegetation may similarly permit wild crucifers in natural habitats to escape or reduce the risk of discovery by searching insects (Feeny, 1976).

Plants of the genus *Dentaria* differ from more typical crucifers in several respects. They are perennial and form patches, often of substantial area, among the ground vegetation of mature deciduous forests. The plants leaf out very early in the spring and approach senescence by the time the forest canopy has leafed out. Plants of *D. diphylla* were damaged heavily, after transplanting into open field habitats, by the typical open-habitat crucifer flea beetles *P. cruciferae* and *P. striolata* (Hicks & Tahvanainen, 1974) and *Dentaria* leaves supported better growth of *P. rapae* larvae than did those of any other crucifer tested (Slansky & Feeny, 1977). Though subject to their own specialized enemies, such as the butterfly *Pieris virginiensis* and the flea beetle *Phyllotreta bipustulata*, *Dentaria* species have probably benefited by their escape, in evolutionary time, into a habitat which is atypical of crucifers and thus not frequented by many of the typical crucifer-adapted enemies.

PLANT-FINDING ADAPTATIONS

Many crucifer-adapted insects have evolved behavioral responses to glucosinolates or their breakdown products, thus permitting them to find their food-plants more easily and to discriminate them from other vegetation. An early example of such behavior was described by Verschaffelt (1911) who found that larvae of *P. brassicae* and *P. rapae* can be stimulated to feed on normally rejected plants by treating the plants with solutions of allylglucosinolate. A recent review by Schoonhoven (1972) lists a dozen insect species which are known to make use of these compounds as behavioral cues. There is even a crucifer-adapted fungus, *Plasmodiophora brassicae*, the spores of which are stimulated to germinate by the presence of allylisothiocyanate (Hooker et al., 1945). Behavioral responses to glucosinolates or isothiocyanates by individuals of any one insect species usually depend on concentration and may also vary from one compound to another (e.g., Thorsteinson, 1953; Hicks, 1974; Finch & Skinner, 1974).

The crucifer-feeding flea beetles, *Phyllotreta cruciferae* and *P. striolata*, are strongly attracted to traps containing solutions of allylisothiocyanate (Feeny et al., 1970) and can also be induced to eat bean leaves, which they normally reject, when these have been cultured in solutions of allylglucosinolate (Hicks,

1974). We have found recently that addition of vials containing solutions of allylglucosinolate in mineral oil to 3-plant islands of *Brassica nigra*, planted among diverse vegetation, greatly accelerated the rate of discovery of the plants by these flea beetles (P. Feeny, J. Gaasch and L. Contardo, in preparation). This finding not only confirms the effectiveness of allylisothiocyanate as a host-finding attractant but also shows that leakage of such compounds, even in small amounts, can be a liability to *B. nigra* plants since it increases their apparency to adapted enemies.

SECONDARY DEFENSE IN CRUCIFERS

Many crucifers are known to contain other secondary compounds in addition to glucosinolates. The genera *Erysimum* and *Cheiranthus*, for example, contain cardenolides, the genus *Iberis* contains cucurbitacins, and plants of the genera *Lunaria* and *Capsella* contain alkaloids (Gheorghiu et al., 1959; Hegnauer, 1964). The genera *Lepidium* and *Thlaspi* contain atypical enzymes which break down glucosinolates not to the typical isothiocyanates but to their corresponding geometrical isomers, the thiocyanates (Gmelin & Virtanen, 1959).

Many of these plants are avoided by crucifer-adapted insects or, if fed upon, support unusually poor growth. Larvae of *P. rapae*, for instance, grow poorly on *Thlaspi arvense*, *Lepidium virginicum*, and *Lunaria annua* (Slansky & Feeny, 1977); they will refuse to eat leaves of *Erysimum cheiranthoides* and *Capsella bursa-pastoris* (A. M. Shapiro, personal communication). Verschaffelt (1911) found that *C. bursa-pastoris* was attacked only very slightly by larvae of *P. rapae* and *P. brassicae*; *E. perofskianum* was also less preferred by these larvae relative to most other crucifers offered to them. Plants of *E. cheiranthoides*, *C. bursa-pastoris*, and *Iberis amara* are not eaten by *P. cruciferae* flea beetles (Feeny et al., 1970). Chew (1975) found that larvae of *Pieris napi macdunnoughii* in Colorado refused to eat *Erysimum asperum*. Larvae of *P. napi macdunnoughii* grew normally on *Thlaspi montanum*, a native plant in Colorado, but they and larvae of *P. occidentalis* died after eating *T. arvense*, an introduced species. The unusual resistance of plants of these genera to typical crucifer enemies may result from their content of atypical secondary compounds (see Verschaffelt, 1911). Allylthiocyanate, for example, is known to be toxic to insects (Brown, 1951). Such compounds could have been evolved as a "second line of defense" in response to enemies which have evolved mechanisms for tolerating glucosinolates and their typical hydrolysis products. Diversification of secondary chemistry, in other words, may permit escape from certain enemies in evolutionary time, at least until further counteradaptations are evolved by the associated insects or other enemies.

In addition to their possible toxic or growth-inhibitory effects, unusual secondary compounds may further benefit a plant species by reducing apparency to adapted enemies. Hydrolysis of allylglucosinolate in leaves of *Thlaspi arvense* yields allylthiocyanate instead of the more typical allylisothiocyanate (Gmelin & Virtanen, 1959; P. Feeny and L. Contardo, in preparation). Three-plant islands of *T. arvense* were colonized by *Phyllotreta* flea beetles at a considerably slower rate than were nearby islands of *Brassica nigra*, perhaps because allyliso-

thiocyanate is an attractant to the beetles whereas allylthiocyanate is not. Colonization of *T. arvense* islands was accelerated by addition of vials containing solutions of allylisothiocyanate (P. Feeny, J. Gaasch and L. Contardo, in preparation).

Crucifers may derive additional protection from adapted enemies as a result of association with plants of different chemistry. Tahvanainen & Root (1972) have found that odors from tomato, *Lycopersicon lycopersicum* (=*esculentum*), and ragweed, *Ambrosia artemisifolia*, plants interfered with the ability of *P. cruciferae* flea beetles to find crucifer host-plants. The reduction of plant apparency to enemies by neighboring plants of different species is an important component of "associational resistance" (Tahvanainen & Root, 1972)—a phenomenon frequently exploited by organic gardeners.

CHEMICAL DEFENSE AND THE HUMAN DIET

The defensive ecology of crucifers seems to typify that of many ephemeral herbaceous plants—plants which rely to a great extent on being hard to find (unapparent) in natural habitats. Such plants seem to contain rather low concentrations of effective toxins. They probably benefit from a diversity of chemical defense in any one species and from association with other plants of different chemistry (Rhoades & Cates, 1976; Feeny, 1976). Their defenses clearly differ from those of the mature foliage of more persistent plants such as shrubs and trees. Such plants are bound to be found by enemies and must correspondingly be well defended; they often contain large amounts of general growth-inhibitory compounds, like tannins, resins and silica, which are resistant to simple counter-adaptation. The foliage of apparent plants is usually tough and deficient in nutrients and water when compared with that of most herbaceous plants (Rhoades & Cates, 1976; Feeny, 1976).

These differences in the defensive ecology of plants, depending upon their apparency to enemies, seem to be reflected in human food preferences. One hundred students in the general ecology course at Cornell University were asked to list as many species of human food-plants as they could think of in 15 minutes. Their total of 108 species, excluding plants used primarily as spices and drugs, was then tabulated by plant growth form and by what part of the plant is eaten (Fig. 1 and Appendix). Though undoubtedly a biased view of more general patterns of plant consumption by man, this survey revealed some interesting and suggestive trends.

Most of the species listed are harvested only for their fruits or seeds, and of these species most are trees (Fig. 1). The production of fleshy fruits is probably an adaptation for seed dispersal by vertebrate animals, including our primate ancestors. Ripe fruits are adapted to be attractive to animals by their size, color, and taste; fruit-eating behavior by the animals is probably reinforced by the fact that fruits contain not only energy-rich carbohydrates and fats but also vitamins and mineral ions which are vital for the survival of many vertebrate animals and not readily available from other natural sources (see McKey, 1975). One can even speculate that our "sweet tooth," now a conspicuous liability in times of readily available sugar, represents a physiological adaptation which

Tree

0   0   38

Shrub or perennial vine

4   1   13

Herb

12   16   16

Grass

0   3   8
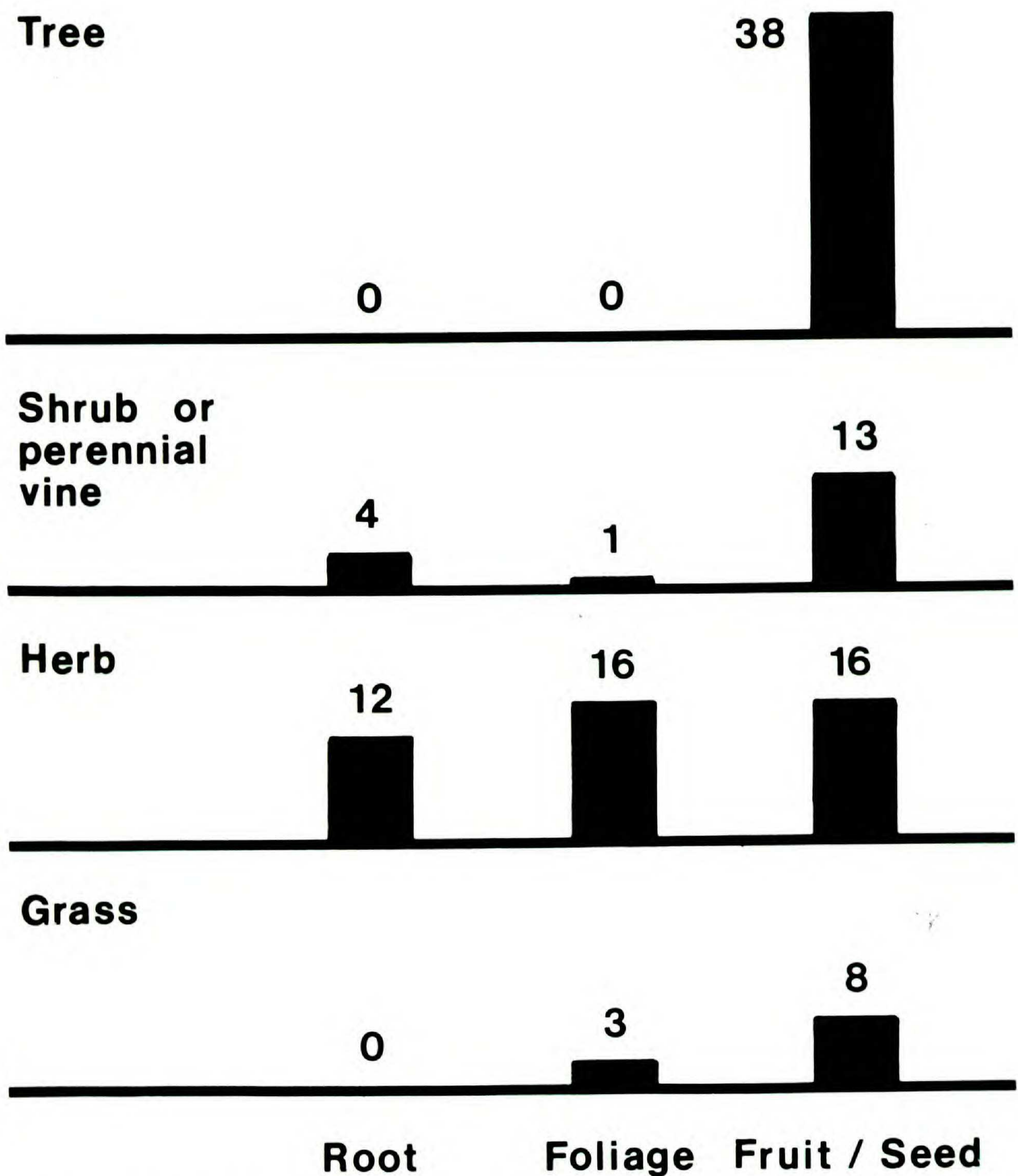
Root   Foliage   Fruit / Seed

FIGURE 1. Distribution of 108 species of human food-plants according to plant growth form and part of plant eaten. Figures indicate number of food-plants listed in each category (3 species listed twice). See Appendix for details.

stimulated our ancestors to seek out fruits with their high nutrient value (see Yudkin, 1969).

A second striking pattern reflected in this survey is that plants whose roots or leaves form part of the human diet are almost all herbs (Fig. 1). These are the plants, including the ancestors of our cruciferous vegetables, which tend to be ephemeral and unapparent in nature. The origins of cultivated plants from herbaceous species were probably due to the concentrated food value of the roots or tubers of many of these species and to the unique preadaptations of

"weedy" plants to thrive in the disturbed habitats associated with human habitation (Hawkes, 1969). Preferential consumption of herbaceous species may also reflect the presence in trees and shrubs of extensive chemical and physical defenses, evolved by trees and shrubs because they are relatively apparent to natural enemies. Many of the drugs and spices used by man come from the foliage and roots of trees and shrubs, though they are rarely consumed in large quantities. By contrast we are presumably able to tolerate the comparatively low concentrations of defensive compounds in crucifers and other herbaceous plants both because of the detoxication enzymes concentrated in the vertebrate liver (Freeland & Janzen, 1974) and also, since the cultural evolution of the use of fire, because we further detoxify or remove many of these compounds by cooking (Yudkin, 1969; Leopold & Ardrey, 1972). Only because they contain relatively small concentrations of toxins can we consume such plants in large quantities.

Apparency and Agriculture

The effectiveness of natural plant defenses is reduced by present agricultural methods. When they are planted in monocultures, crop plants become more apparent to natural enemies than are their ancestors in nature, yet they possess chemical and physical defenses inappropriate for survival as apparent plants. This is a major reason that substantial quantities of synthetic pesticides are often required to prevent widespread devastation of crops.

It would undoubtedly be possible to modify crop varieties and agricultural methods so as to mimic the defensive ecology of wild ancestral plants more closely. Levels of natural defensive compounds could be maintained or restored by selective plant breeding and emphasis placed on diversity of defense within any particular crop species. Plant apparency could be reduced by such traditional techniques as crop rotation and interplanting of different crops or chemical varieties of any one crop. Apparency could be reduced further by eliminating or modifying those plant chemicals which the more important plant enemies use as behavioral attractants or feeding stimulants.

Strategies to improve and diversify chemical resistance would be more effective if they were coordinated with strategies to reduce plant apparency. Just as the evolution of resistance to a particular pesticide by an insect population may result from extensive and repeated exposure to that compound, so also the fewer the insects which find a particular plant variety, the less likely they are to evolve methods of tolerating the plant's chemical defenses (Southwood, 1973).

A key component of the defensive ecology of crucifers and other unapparent plants seems to be chemical diversity in space and time (Rhoades & Cates, 1976; Futuyma, 1976; Feeny, 1976). The more closely we can simulate this diversity in our fields of vegetable crops, the less dependent are we likely to become on the use of synthetic pesticides to achieve a given level of agricultural production.

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APPENDIX

Species of human food-plants listed by 100 students in the general ecology course (Bio. Sci. 360, Fall 1976) at Cornell University, and categorized as a function of: (1) Growth form of plant and (2) Part of plant eaten. Bulbs and tubers are included with roots; shoots, stems and flower parts are included with foliage. Three species (*Vitis vinifera, Beta vulgaris,* and *Brassica rapa*) are listed twice. an. = annual, bien. = biennial, per. = perennial.

A. TREES
    (i) *Root*: No species listed.
    (ii) *Foliage*: No species listed.
    (iii) *Fruit*:

Mango	*Mangifera indica*	tree	Anacardiaceae
Pawpaw	*Asimina triloba*	small tree	Annonaceae
Papaya	*Carica papaya*	small tree	Caricaceae
Japanese persimmon	*Diospyros kaki*	tree	Ebenaceae
Avocado	*Persea americana*	tree	Lauraceae
Fig	*Ficus carica*	tree	Moraceae
Breadfruit	*Artocarpus altilis*	tree	Moraceae
Banana, plantain	*Musa acuminata* and	tall per. herb	Musaceae
	Musa ×*paradisiaca*	tall per. herb	Musaceae
Common guava	*Psidium guajava*	small tree	Myrtaceae
Olive	*Olea europaea*	tree	Oleaceae
Date	*Phoenix dactylifera*	tall palm	Palmaceae
Pomegranate	*Punica granatum*	small tree	Punicaceae
Quince	*Cydonia oblonga*	small tree	Rosaceae
Apple	*Malus pumila*	tree	Rosaceae
Pear	*Pyrus communis*	tree	Rosaceae
Apricot	*Prunus armenica*	small tree	Rosaceae
Sweet cherry	*Prunus avium*	tree	Rosaceae
Plum	*Prunus domestica*	small tree	Rosaceae
Peach, nectarine	*Prunus persica*	small tree	Rosaceae
Sweet orange	*Citrus sinensis*	tree	Rutaceae
Grapefruit	*Citrus* ×*paradisi*	small tree	Rutaceae
Nagami kumquat	*Fortunella margarita*	small tree	Rutaceae

    (iv) *Seed*:

Cashew	*Anacardium occidentale*	tree	Anacardiaceae
Pistachio	*Pistacia vera*	small tree	Anacardiaceae
European filbert/hazelnut	*Corylus avellana*	small tree	Corylaceae
American filbert/hazelnut	*Corylus americana*	small tree	Corylaceae
European chestnut	*Castanea sativa*	tree	Fagaceae
Beech	*Fagus grandifolia*	tree	Fagaceae
Pecan	*Carya illinoensis*	tree	Juglandaceae
Hickory	*Carya ovata* and	tree	Juglandaceae
	Carya laciniosa	tree	Juglandaceae
Butternut	*Juglans cinerea*	tree	Juglandaceae
English walnut	*Juglans regia*	tree	Juglandaceae
Brazil nut	*Bertholletia excelsa*	tree	Lecythidaceae
Coconut	*Cocos nucifera*	tall palm	Palmaceae
Piñon	*Pinus cembroides*	tree	Pinaceae
Almond	*Prunus dulcis*	small tree	Rosaceae

B. SHRUBS AND PERENNIAL VINES

    (i) *Root*:

Sweet potato (tuber)	*Ipomoea batatas*	per. vine	Convolvulaceae
Yam	*Dioscorea* spp.	per. vine	Dioscoreaceae
Cassava/manioc	*Manihot esculenta*	shrub	Euphorbiaceae
Ground nut (tuber)	*Apios americana*	per. vine	Leguminosae

    (ii) *Foliage*:

European grape	*Vitis vinifera*	per. vine	Vitaceae

APPENDIX. (continued)

(iii) *Fruit*:

American elder	*Sambucus canadensis*	shrub	Caprifoliaceae
Huckleberry	*Gaylussacia* spp.	shrub	Ericaceae
Cranberry	*Vaccinium macrocarpon*	shrub	Ericaceae
Blueberry	*Vaccinium* spp.	shrub	Ericaceae
Passion fruit/purple granadilla	*Passiflora edulis*	per. vine	Passifloraceae
Red raspberry	*Rubus idaeus*	shrub	Rosaceae
Black raspberry	*Rubus occidentalis*	shrub	Rosaceae
Loganberry, boysenberry	*Rubus ursinus*	shrub	Rosaceae
Rose hip	*Rosa villosa*	shrub	Rosaceae
American gooseberry	*Ribes hirtellum*	shrub	Saxifragaceae
Red currant	*Ribes sativum*	shrub	Saxifragaceae
Fox grape	*Vitis labrusca*	per. vine	Vitaceae
European grape	*Vitis vinifera*	per. vine	Vitaceae

(iv) *Seed*: No species listed.

C. HERBACEOUS PLANTS
    (i) *Root*:

Onion (bulb)	*Allium cepa*	per.	Amaryllidaceae
Beet, sugar beet	*Beta vulgaris*	an./bien.	Chenopodiaceae
Rutabaga	*Brassica napus*	an./bien.	Cruciferae
Turnip	*Brassica rapa*	an./bien.	Cruciferae
Radish	*Raphanus sativus*	an./bien.	Cruciferae
Burdock	*Arctium lappa*	per.	Compositae
Jerusalem artichoke (tuber)	*Helianthus tuberosus*	per.	Compositae
Camass (bulb)	*Camassia quamash*	per.	Liliaceae
Potato (tuber)	*Solanum tuberosum*	per.	Solanaceae
Cattail	*Typha* spp.	per.	Typhaceae
Carrot	*Daucus carota*	an./bien.	Umbelliferae
Parsnip	*Pastinaca sativa*	bien.	Umbelliferae

(ii) *Foliage*:

Leek	*Allium ampeloprasum*	bien.	Amaryllidaceae
Comfrey	*Symphytum officinale*	per.	Boraginaceae
Beet	*Beta vulgaris*	an./bien.	Chenopodiaceae
Spinach	*Spinacea oleracea*	an./bien.	Chenopodiaceae
Cabbage, kale, etc.	*Brassica oleracea*	an./bien.	Cruciferae
Chinese cabbage	*Brassica rapa*	an./bien.	Cruciferae
Water cress	*Nasturtium officinale*	per.	Cruciferae
Endive	*Cichorium endivia*	an./bien.	Compositae
Chicory	*Cichorium intybus*	per.	Compositae
Artichoke (flower bud and scales)	*Cynara scolymus*	per.	Compositae
Lettuce	*Lactuca sativa*	an./bien.	Compositae
Dandelion	*Taraxacum officinale*	per.	Compositae
Asparagus (young stem)	*Asparagus officinalis*	per.	Liliaceae
Rhubarb (leaf stalk)	*Rheum rhabarbarum*	per.	Polygonaceae
Celery (leaf stalk)	*Apium graveolens*	bien.	Umbelliferae
Fennel (leaf stalk)	*Foeniculum vulgare*	an./per.	Umbelliferae

(iii) *Fruit*:

Pineapple	*Ananas comosus*	per.	Bromeliaceae
Sunflower	*Helianthus annuus*	an.	Compositae
Watermelon	*Citrullus lanatus*	an. vine	Cucurbitaceae
Melon	*Cucumis melo*	an. vine	Cucurbitaceae
Cucumber	*Cucumis sativus*	an. vine	Cucurbitaceae
Squash, pumpkin, zucchini	*Cucurbita* spp.	an. vine	Cucurbitaceae
Strawberry	*Fragaria* ×*ananassa*	per.	Rosaceae
Green pepper, chili	*Capsicum annuum*	an./per.	Solanaceae

APPENDIX. (continued)

Tomato	*Lycopersicon lycopersicum*	an./per.	Solanaceae
Eggplant	*Solanum melongena*	an./per.	Solanaceae
(iv) *Seed*:			
Peanut	*Arachis hypogaea*	an.	Leguminosae
Soybean	*Glycine max*	an.	Leguminosae
Lentil	*Lens culinaris*	an.	Leguminosae
Lima bean	*Phaseolus limensis*	an./per.	Leguminosae
Kidney bean	*Phaseolus vulgaris*	an.	Leguminosae
Garden pea	*Pisum sativum*	an. vine	Leguminosae

D. GRASSES
  (i) *Root*: No species listed.

  (ii) *Foliage*:

Bamboo (young shoots)	*Phyllostachys* spp. and	per.	Gramineae
	Bambusa spp.	per.	Gramineae
Sugar cane (stems)	*Saccharum officinarum*	per.	Gramineae

  (iii) *Fruit*: No species listed.
  (iv) *Seed*:

Oat	*Avena sativa*	an.	Gramineae
Barley	*Hordeum vulgare*	an.	Gramineae
Rice	*Oryza sativa*	an.	Gramineae
Broomcorn/millet	*Panicum miliaceum*	an.	Gramineae
Rye	*Secale cereale*	an.	Gramineae
Sorghum	*Sorghum bicolor*	an.	Gramineae
Common wheat	*Triticum aestivum*	an.	Gramineae
Corn	*Zea mays*	an.	Gramineae